

## HUMAN OCULAR VERGENCE MOVEMENTS INDUCED BY CHANGING SIZE AND DISPARITY

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### SUMMARY

1. Human subjects viewed an electronically generated bright square. Horizontal movements of the two eyes were recorded with the scleral coil method.

2. The dynamic properties of vergence movements induced by movement of the bright square were investigated for the following three kinds of stimulus motion: (a) both the size and the binocular disparity of the square changed together, in such a way as to exactly mimic the retinal image changes produced by a real object's motion in depth; (b) the changing-size component in (a) was present with no disparity component; (c) the changing-disparity component in (a) was present with no size component. The gain and phase of the ocular vergence responses to these three stimuli were computed.

3. Ocular vergence movements were induced by changing size in all five subjects. Responses during binocular viewing were higher and less variable than responses during monocular viewing. Size oscillations induced ocular vergence oscillations with a phase lead of up to 65 deg relative to target size for frequencies of stimulation below 1.0 Hz. Vergence oscillation amplitudes were of the order of 10 min of arc and maximal for frequencies of 0.4–0.7 Hz.

4. Ocular vergence movements were not induced by changes in target size in one dimension nor by flickering a stationary square.

5. Ocular vergence movements induced by size changes were entirely transient with no sustained component: vergence responses to disparity were sustained.

6. When the stimulus combined size change with disparity change in the ratio characteristic of a real moving object, vergence tracking was more accurate and less noisy than when the eyes were stimulated with the disparity component alone.

7. The ocular vergence response induced by the combination of size change with disparity change was accurately predicted by linearly adding the vergence response produced by the size change alone to the vergence response produced by the disparity change alone: combined stimulation produced no evidence of non-linear interaction between responses to size change and to disparity change.

8. The properties of vergence responses induced by changing size and by changing

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disparity showed several close correlations with the corresponding data on psychophysical sensitivity for motion-in-depth sensation.

9. We suggest that responses to changing size contribute to the accuracy with which ocular vergence tracks real objects moving in depth.

#### INTRODUCTION

The motion of a real-world object towards the eyes commonly generates both vergence eye movements and a sensation of motion in depth. A widely accepted way of investigating these phenomena is in terms of the several mathematically separable motion correlates in the object's retinal image; if it can be demonstrated that the responses to these several retinal image changes are approximately independent then, according to this rationale, such an analysis might cast light upon separate functional mechanisms in the visual and oculomotor pathways.

Suppose that an observer looks steadily at a stationary object, and that the object's left and right images are sharply accommodated on the respective foveae. If the object now starts to approach the observer its motion will cause the following four changes in the retinal images to occur: (a) one or both images will move away from the fovea and consequently (b) retinal disparity will progressively increase; (c) the initially sharp images will grow progressively more blurred; (d) retinal image size will progressively increase.

The first three of these four retinal image correlates of object motion in depth have been extensively discussed in the context of vergence eye movements. Attempting to maintain foveation would in itself cause a vergence movement; disparity change is the effective stimulus for 'fusional vergence' (Westheimer & Mitchell, 1956). Accommodation and vergence are linked (Fincham, 1951; Fincham & Walton, 1957); accommodative changes cause vergence changes (Kenyon, Ciuffreda & Stark, 1978). As for the relative effectiveness of disparity and accommodation in driving ocular vergence, disparity has been shown to be considerably stronger (Semmlow & Wetzell, 1979). Comparatively little, however, is known about the role of size in the control of ocular vergence. Static differences in size produce sustained changes in vergence that have been attributed to a cognitive factor, perceived distance (Ittleson & Ames, 1950; Alpern, 1958). However, although changing disparity is generally accompanied by changing size when real-world objects move in depth, research studies on vergence dynamics have so far been restricted to the effects of changing disparity alone; there are no previous reports on the effects on vergence of dynamically changing size, presented either alone or in combination with changing disparity.

In the present study, we compare the dynamics of ocular vergence responses induced by size changes alone with those induced by disparity changes alone, and also with those induced by various combinations of the two, including the unique combination generated by an equivalent real-world object. So far as was possible, our experimental design followed a previous psychophysical study in which visual sensitivity to changing size was compared with visual sensitivity to changing disparity and also to their combinations. In order to further aid a comparison of our present eye movement data with those previous psychophysical findings, we used the

visual display electronics employed in the psychophysical study (Regan & Beverley, 1978, 1979).

To anticipate, we find that, by itself, changing size induces ocular vergence motion. Although vergence responses to size changes alone are considerably weaker than vergence responses to disparity changes alone, the size component may well have a role in the control of ocular vergence in real-world conditions where disparity changes caused by object motion are generally accompanied by size changes: we found vergence tracking to be more accurate and less noisy for changing disparity combined with changing size than for changing disparity alone. The correspondence between vergence responses and psychophysical sensitivity seems to be close: vergence responses to size were rate driven (i.e. transient), while vergence responses to disparity were sustained, paralleling previous psychophysical findings; furthermore, the vergence frequency tuning curves were similar to the corresponding psychophysical curves; for eye movements and psychophysics alike, responses to size and to disparity were substantially independent.

#### METHODS

##### *Subjects*

Five subjects (including the authors) participated in the experiments. All subjects were experienced in oculomotor experiments. H.S. (aged 34 years) was emmetropic. C.E. (aged 35) was myopic and normally wore contact lenses. A.B. (aged 28), D.R. (aged 49) and H.C. (aged 49) were myopic and normally wore spectacles. D.R. and H.C. were presbyopic with little residual accommodation. Corrected visual acuity was 20/20 or better for all subjects.

##### *Recording*

Horizontal eye movements of both eyes were recorded with induction coils mounted in scleral annuli in an a.c. magnetic field using the technique first described by Robinson (1963) as modified by Collewyn, Van der Mark & Jansen (1975). The range of the recording system was adjusted to 4 deg; its dynamic range was d.c. to better than 100 Hz (3 dB down) noise level, less than 6 s of arc and deviation from linearity less than 0.1 %. Head movements were minimized by supports under the chin and around the skull.

##### *Visual stimuli*

One bright square of luminance 4 cd/m<sup>2</sup> was generated on each of two c.r.t. (cathode ray tube) monitors (Tektronix model 604 with green type 31 phosphor). By means of a mirror stereoscope, one square was presented to the left eye and the other to the right eye so that they could be viewed in binocular fusion.

The starting (initial) size of each square was 2 cm side length (0.78 deg subtense), and they were viewed at 145 cm against a dark surround. The squares were generated by special-purpose electronics described previously (Regan & Beverley, 1978, 1979). Two identical, irregular configurations of six red l.e.d.s (light-emitting diodes) were positioned around each of the oscilloscope screens. The two sets of l.e.d.s were easily fused and served as a depth plane of reference. The brightness of the l.e.d.s was adjusted by the subjects so that the brightness of the binocularly fused l.e.d.s was about the same as that of the fused square. The l.e.d.s were used in some of the experiments to investigate whether the presence of reference marks affected ocular vergence movements. Experiments were carried out in a darkened room. No targets were visible other than the stimuli described above. A microcomputer (DEC PDP 11/10) was used for stimulus generation, data collection and data analysis.

Data collection for each subject was spread over several sessions. Each session was limited to a duration of about 30 min during which about forty measurements were recorded. For oscillatory stimulation, each measurement lasted 32.8 s (4096 data points of each relevant signal, sampled at a rate of 125 Hz). The period of recording was half as long for ramp stimuli.

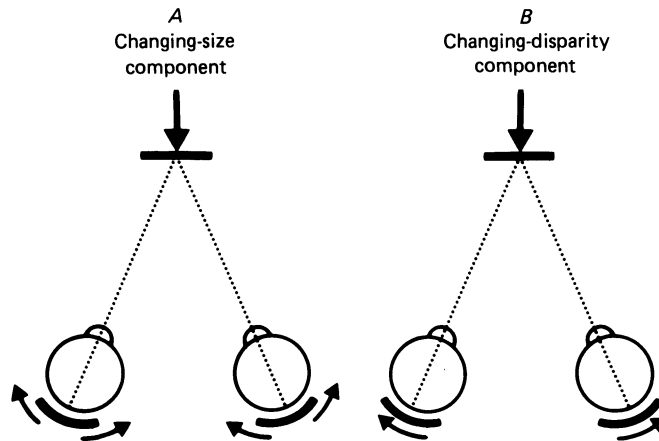


Fig. 1.  $\downarrow$  represents a binocularly fused, rigid, non-rotating object moving in depth directly towards an observer whose eyes maintain a constant angle of convergence. The retinal image motion caused by the object's motion is the vector sum of two components: *A*, a rate of increase of size; *B*, a translation of the images in opposite directions at velocities whose difference is equal to the rate of change of disparity.

TABLE 1. Initial and extreme values of the stimulus parameters for combined changes of size and disparity, for size change alone and for disparity change alone

Stimulus	Equivalent distance of a real square object (cm)	Angular size (deg)	Target vergence of the fused square (deg)
Size change	147 ('initial')	0.78	2.5
	73.5 ('approach')	1.56	2.5
	294 ('recession')	0.39	2.5
Disparity change	147 ('initial')	0.78	2.5
	73.5 ('approach')	0.78	5.1
	294 ('recession')	0.78	1.3
Combined changes of size and disparity	147 ('initial')	0.78	2.5
	73.5 ('approach')	1.56	5.1
	294 ('recession')	0.39	1.3

The sensitivity of the eye movement recorder was calibrated at the start of each session: calibration targets containing three fixation marks spaced at 1.0 deg intervals were presented to each eye separately, and the subject fixated on each mark in turn while eye movements were recorded.

The following three kinds of stimuli were used: (1) the squares progressively doubled in size while simultaneously translating in opposite directions so as to simulate an approach (Fig. 1), or progressively decreased in size by a factor of 0.5, while simultaneously translating so as to simulate a recession. The ratio between the velocity of translation and the rate of change of size was always equal to the unique ratio appropriate to a real object 2 cm wide by an observer with a 6.5 cm interpupillary separation. The relevant computation is given in Regan & Beverley (1979, appendix 1). Table 1 gives the square's linear dimensions and the target vergence at the start and the end of a simulated approach, and at the start and end of a simulated recession; (2) the second kind of stimulus was the same as (1) except that the translational component was zero; (3) the third kind was the same as (1) except that the changing-size component was zero.

Sinusoidal and triangular wave forms of 0.2, 0.4, 0.7, 1.0 and 2.0 Hz were used for oscillatory stimulation. For sinusoidal and triangular wave modulations of size, the positions of the square's edges followed a sinusoidal or triangular wave time course. The type of stimulation (changing size, changing disparity or both in combination), the direction of stimulus motion (equivalent to an approach or a recession from the start position) and the frequency of oscillation were interleaved and sequenced in a random order. In the case of transient stimulation with ramps, the subject was presented with a stimulus which changed in size and/or target vergence from the initial to one of the two final positions. After a period of 8 s, during which the stimulus remained stationary, it was reset stepwise to the starting position. The ramp velocities were the same as the velocities of the square with oscillating triangular wave stimulation.

We envisaged that, if size changes were capable of inducing ocular vergence movements, then these vergence movements would create disparity between the retinal images of the squares. Disparity, in its turn, might induce vergence movements counteracting those resulting from changing-size stimulation. Therefore, we did additional experiments with changing-size stimuli while the visual-oculomotor loop for binocular disparity was opened. This was achieved by coupling half of the difference of the two horizontal eye positions to the horizontal position of each square, so that ocular vergence movements could be executed without inducing concomitant binocular disparity. However, ocular version movements remained unaffected. Such open-loop vergence experiments were also done with one-dimensional oscillation of only the height or only the width of the square. Finally, to test for any effects of luminous flux, we presented stationary squares whose luminance oscillated by a factor 4 (between 2 and 8 cd/m<sup>2</sup>) at frequencies of 0.2, 0.4, 0.7, 1.0 and 2.0 Hz.

#### *Data analysis*

Horizontal eye position signals were digitized on-line at a frequency of 125 Hz (resolution 4.4 s of arc, 8 ms) after low-pass filtering with a cut-off frequency of 62.5 Hz, and then stored on disk. In the off-line analysis, eye position signals were first recalibrated using the calibration recordings made at the beginning of each session. The errors in gain and offset between target and eye were calculated and the complete set of data was corrected on this basis. This procedure also corrected for any magnification or reduction factors caused by the subjects' spectacles.

Target vergence of the square (defined as the angle between a line passing through the centre of one square and the nodal point of the eye viewing that square and a similar line for the other eye) was calculated from the experimental data by subtracting the position of the centre of the right square from the position of the centre of the left square. Ocular vergence was calculated in a similar way by subtracting the right horizontal eye position from the left horizontal eye position. Zero values correspond to binocular fixation of a point at a distance of 147 cm (true vergence angle 2.53 deg of convergence).

It was difficult to suppress blinks during the entire duration of the measurement. Blinks cause a considerable transient convergence (Collewijn, Van der Steen & Steinman, 1985) which would interfere with the subsequent analysis. Therefore, software was developed to detect the blinks and remove the resulting transient convergence from the ocular vergence signal. The detection of the start of blinks was based upon velocity and acceleration criteria. Velocity profile and blink duration limits were used to detect the end of the blinks and to check whether the detected event was a true blink. The blinks were then removed from the ocular vergence signal and the missing parts were filled with zero-velocity elements. Saccades were relatively rare and sufficiently conjugate that they did not contaminate the vergence signal to any significant extent.

The vergence error (i.e. binocular disparity) was calculated by subtracting the ocular vergence from the target vergence. For sinusoidal stimulus movements, the recordings of ocular vergence, target vergence, and target size were analysed by discrete Fourier analysis using a fast Fourier transform algorithm, then gain (ratio of peak-to-peak amplitudes) and phase (in degrees) between the fundamental frequency components of ocular vergence and target vergence (or target size) were calculated by means of auto- and cross-power spectral densities. Vergence movements were taken to be in phase with the inducing changes of size if the maximum square size coincided with the maximum convergence.

## RESULTS

*Vergence responses to oscillations of target size*

Fig. 2 shows examples of ocular vergence movements induced by a pure changing-size display viewed with both eyes. Oscillating the size of the squares induced vergence oscillations of amplitude between 2 and 16 min of arc peak-to-peak. The largest vergence oscillations were induced by an oscillation frequency of about 0.5 Hz; and oscillation amplitude progressively fell as frequency was increased beyond 0.5 Hz, though vergence responses were still well above noise level at a

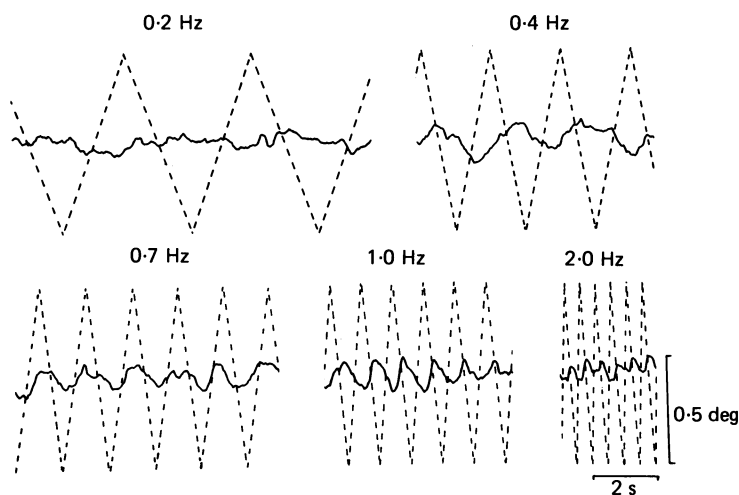


Fig. 2. Examples of ocular vergence movements (continuous lines) induced by oscillations in target size (dashed lines). Ocular convergence is denoted by downward movement and magnification of the target size is indicated by upward movement of the appropriate signals. Viewing was with both eyes. The target squares oscillated in angular size between 1.56 deg and 0.78 deg side length. The 0.5 deg calibration is for both signals.

frequency of 2.0 Hz. Fig. 3 plots response amplitude and phase as a function of frequency. Each data point is the mean for five subjects. The amplitude of the vergence responses peaked at 0.4 Hz. Subject-to-subject variability was largest at 0.2 Hz. Surprisingly, the phase of the ocular vergence response showed a lead for the lower frequencies. The phase lead was most marked at a frequency of 0.2 Hz where it amounted to a mean value of 65 deg.

The possibility that ocular vergence was more directly related to the velocity of change of target size than to size itself was examined by shifting the calculated phases backwards over 90 deg (Fig. 3). This shifted response lagged the velocity of the size change at all frequencies. These phase lags were well fitted by a linear function ( $r^2 = 0.91$ , where  $r$  is the coefficient of correlation) representing a pure delay of 204 ms of the ocular vergence movements relative to the rate of change of target size. The presence or absence of reference marks (i.e.d.s) had no appreciable effect on the size-induced vergence oscillations.

One eye was occluded while viewing the changing-size stimulus, and Fig. 4 shows

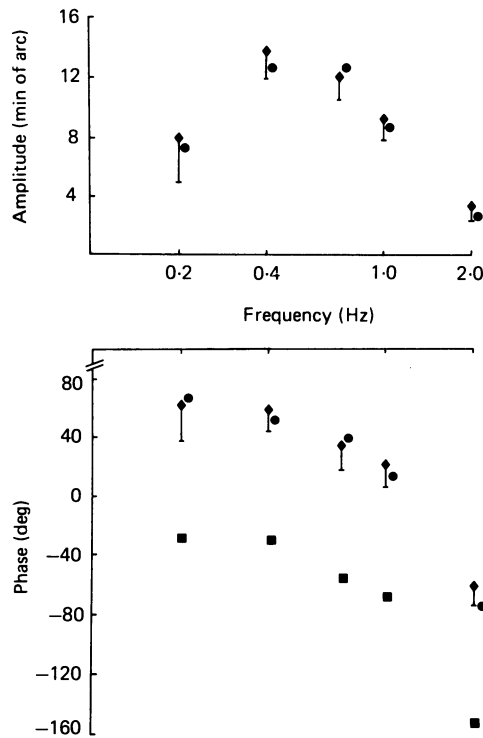


Fig. 3. Amplitude and phase of ocular vergence responses induced by changes in target size. Eye movements were recorded under closed-loop (diamonds) and open-loop (circles) conditions for disparity. The phase of ocular vergence responses relative to the rate of change of stimulus size is indicated by squares. Each point plots the mean for five subjects, and vertical bars show one standard deviation. Viewing was with both eyes.

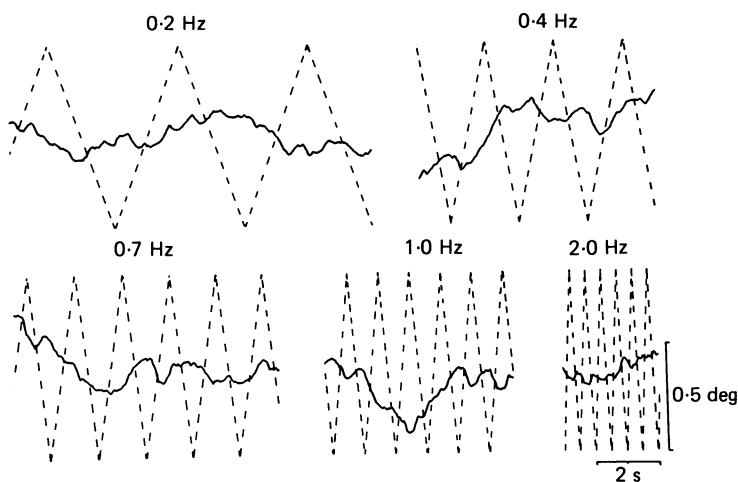


Fig. 4. The continuous lines give examples of ocular vergence movements induced by oscillations of target size indicated by the dashed lines. Conventions as in Fig. 2. Viewing was monocular.

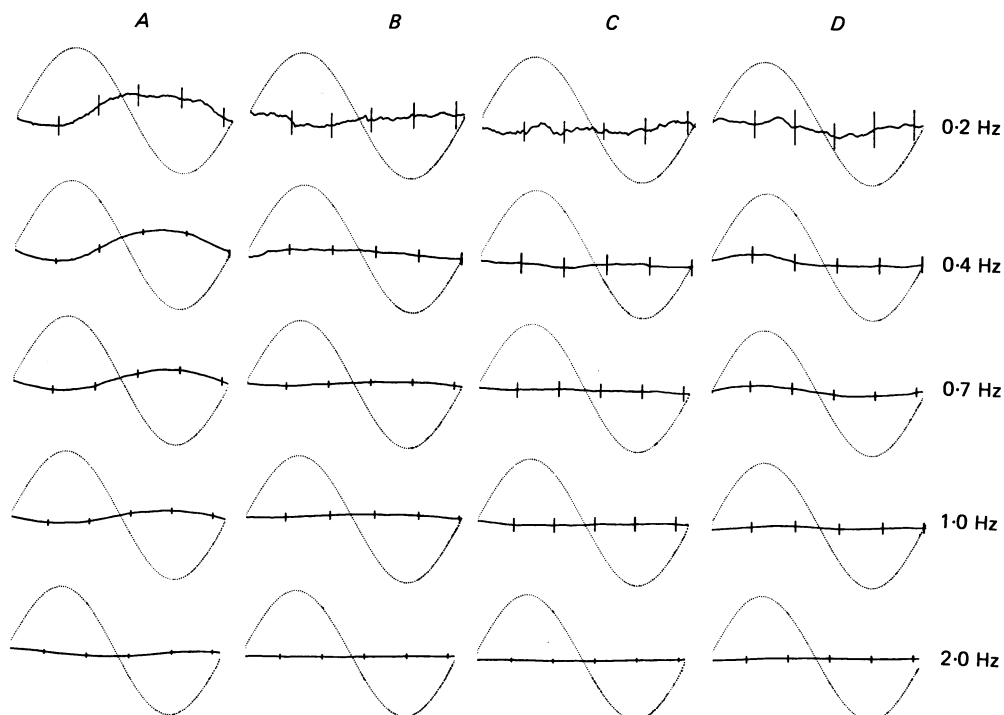


Fig. 5. Ocular vergence responses (continuous lines) to changing-size (*A*), changing-width (*B*), changing-height (*C*), and flicker (*D*) stimulation (dotted lines). Other conventions as in Fig. 2. All responses were obtained from one subject who viewed the squares with both eyes. The signal-to-noise ratio of the eye movement records was enhanced by averaging for 32.8 s (six to sixty response cycles, depending on the frequency). The vertical lines in the ocular vergence traces indicate standard deviations. Note the different time scales for the different frequencies of stimulation.

that the resulting monocular responses were smaller and more irregular compared with the Fig. 2 responses to size oscillations viewed with both eyes. Fig. 4 also shows that ocular vergence was somewhat unstable when it was not controlled by disparity: when one eye was occluded, substantial wanderings of vergence of up to 1 deg peak-to-peak occurred in addition to the stimulus-correlated vergence oscillations; these wanderings seemed to be unrelated to the stimulus.

The fact that a change in square size produced a vergence response does not necessarily imply that the response was specific to the change in retinal image size *per se*. For example, in one study it was found that almost all neurones encountered in cat visual cortex responded to changing-size stimulation, but qualitative control experiments showed that 34 % of these cells were actually responding to changes of light flux associated with the size changes, rather than responding to the size changes themselves (Regan & Cynader, 1979). In the present experiment, our stimuli were presented at constant luminance, so that size changes were correlated with changes of total light flux. It might be thought that the potential artifact of flux-related responses could have been avoided by presenting stimuli at constant light flux.



However, this would have caused luminance changes which correlated with size changes, so that neurones whose receptive fields were smaller than the stimulus square would still have received a varying light flux. In order to control for the possibility that the observed vergence responses induced by changing size were artifactually caused by changes of light flux rather than by the size changes *per se*, we recorded vergence movements while flickering the squares, but with square size and disparity held constant. We found that vergence responses to flicker seldom exceeded 1 min of arc peak-to-peak, and so were negligibly small compared with vergence responses to oscillating size (compare Fig. 5D with Fig. 5A). The increased noise at 0.2 Hz evident in Fig. 5D was probably due to the small number of cycles ( $n = 6$ ) averaged at this frequency.

*Responses to size-change stimulation during open-loop conditions for disparity*

In the previous section our intent was to find whether vergence movements were induced by size changes that were unaccompanied by changes of disparity. If regarded in purely optical terms our stimulus seems appropriate: the c.r.t.-generated squares oscillated in size with no side-to-side translation. It is tempting to conclude that we had achieved our aim of pure changing-size stimulation unaccompanied by changes in disparity, but unfortunately this is not so. Because the two c.r.t.-generated squares did not translate from side to side, the physiological stimulus included a changing-disparity component: size oscillations induced vergence oscillations, and in turn these eye movements caused the disparity of the squares to oscillate, even though the squares were stationary.

It might, therefore, seem surprising that, in normal viewing conditions, changing size produced any appreciable vergence motion at all: on the face of it, one might expect that any vergence response induced by changing size would be largely cancelled by the much stronger changing-disparity signal. We will return to this point later.

In order to generate a stimulus that, in physiological rather than optical terms, could be described as pure 'changing size' unaccompanied by disparity changes, we proceeded as follows. Our problem was to prevent the creation of disparity changes by the vergence eye movements induced by size changes. As described in the Methods, we fed the eye movement signal to the stimulus display, so that the squares translated from side to side, exactly matching the eye movements and maintaining zero disparity independently of vergence oscillations.

Fig. 3 shows the amplitude and phase of vergence oscillations induced by size oscillations under these open-loop conditions for disparity. The computed values lay within the range of variability of corresponding values obtained in normal (i.e. closed-loop) viewing conditions. This implies that the ocular vergence response to oscillating size was not significantly affected by stimulus-induced changes of binocular disparity.

We should add that the open-loop condition proved to have two major disadvantages. First, when ocular vergence was not controlled by binocular disparity it was as markedly unstable as during monocular viewing (Fig. 4). Secondly, blinks caused a shift of ocular vergence that persisted for several seconds, while it returned slowly towards the position it had prior to the blink. Under open-loop conditions, this

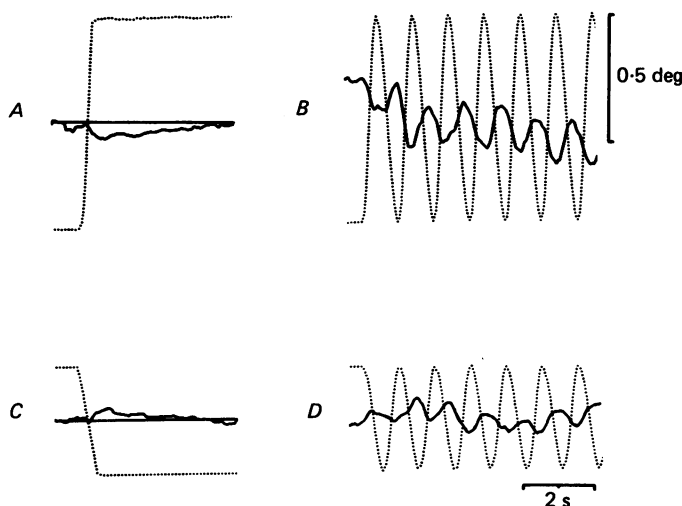


Fig. 6. *A* and *C*, ocular vergence movements (continuous lines) induced by ramping changes of size (dotted lines). *A*, size increase; *C*, size decrease. *B* and *D*, size oscillations between the same extremes of size as in *A* and *C* respectively. The signal-to-noise ratio of the eye movement records was enhanced by signal averaging; each record shown is the mean of ten samples.

recovery took up to 10 s. Nevertheless, this instability of ocular vergence and blinks did not substantially affect the computed gain and phase of ocular vergence during stimulation with oscillating size because these artifacts were not correlated with the frequency of stimulation.

#### *Vergence movements induced by ramp changes of size*

Vergence responses to ramp changes of size were recorded from the two subjects who gave the largest responses to oscillatory stimulation. Responses to ten ramps were computer averaged in order to enhance the signal-to-noise ratio of the eye recordings. Fig. 6*A* and *C* shows that these averaged vergence responses were entirely transient, and had died away completely after about 3 s.

Fig. 6*B* shows vergence responses to the first few cycles of a size oscillation whose rate of change of size was adjusted to match the rate of change of size in the Fig. 6*A* ramp, and Fig. 6*D* shows vergence responses to size oscillations whose rate of change of size matched that of the Fig. 6*C* ramp. It is evident that the oscillatory response did not assume its maximum amplitude immediately at the start of stimulation, but took some time to build up to its 'steady state' value. This is a familiar phenomenon in the oscillatory response of physical systems; in mechanical or electrical linear resonant systems, for example, it is well known that the number of response cycles required to gradually build up the response depends on the selectivity ( $Q$  factor) of the frequency tuning curve. Because the vergence response of Fig. 6*B* and *D* shows this build-up phenomenon, it is appropriate to compare the amplitude of the ramp response with the oscillatory response amplitude during the first half-cycle, rather than with the steady-state oscillatory response amplitude after build-up. It can be seen from Fig. 6 that the ramp response has approximately the same amplitude as the oscillatory response during the first half-cycle.

TABLE 2. Peak-to-peak amplitudes of ocular vergence movements induced by oscillations of size, height and width and by flicker stimulation. Means and standard deviations, in minutes of arc, are shown for five subjects

Frequency (Hz)	Size	Height	Width	Flicker
0.2	$7.9 \pm 3.0$	$1.6 \pm 0.6$	$1.6 \pm 0.8$	$1.7 \pm 0.8$
0.4	$13.9 \pm 1.8$	$1.0 \pm 0.4$	$0.9 \pm 0.7$	$1.1 \pm 0.5$
0.7	$12.1 \pm 1.6$	$0.9 \pm 0.5$	$0.7 \pm 0.4$	$1.2 \pm 1.1$
1.0	$9.2 \pm 1.5$	$0.6 \pm 0.2$	$0.6 \pm 0.2$	$0.7 \pm 0.4$
2.0	$3.3 \pm 1.2$	$0.2 \pm 0.1$	$0.1 \pm 0.1$	$0.3 \pm 0.3$

We conclude that the ramp data directly demonstrate the absence of any sustained component in the vergence response induced by changing size, and that the amplitude of the ramp response is qualitatively consistent with a low-selectivity (i.e. low- $Q$ ) resonant-like characteristic of the vergence response to size oscillations, and with the bandpass nature of the frequency tuning plot shown in Fig. 3.

#### *Vergence responses to one-dimensional changes in size*

Vergence responses to change of size in one dimension were investigated under closed-loop and open-loop conditions for disparity. In this experiment the height of the stimulus squares was increased and decreased by a factor of two while width was held constant, or width was varied similarly while height was held constant. Signal averaging was used in order to retrieve any stimulus-induced vergence responses that were too small to be distinguished in the raw data.

Fig. 5 shows typical results for the open-loop vergence condition; the results for closed-loop conditions were similar. Although ocular vergence was driven by isotropic changes of target size (Fig. 5*A*), vergence was not affected by changes in height alone or in width alone (Fig. 5*B* and *C*). The mean amplitudes of the responses to the different types of stimulation are shown in Table 2.

Table 2 shows that ocular vergence responses to changes of height or width were mostly smaller than 1 min of arc. The amplitudes as well as the standard deviations of the responses decreased with increasing frequency. This indicates that large parts of the responses were not caused by the stimulus, but rather were due to noise and uncorrelated vergence movements. The increased noise at 0.2 Hz is probably due to the smaller number of cycles ( $n = 6$ ) averaged at this frequency.

#### *Changes of size and of disparity combined*

In order to estimate the contribution of the size change to the ocular vergence movements induced by the motion of real-world objects, we compared vergence oscillations induced by a combination of size and disparity change with vergence oscillations induced by the changing-disparity component alone. Fig. 7 shows mean gain and phase as a function of frequency for five subjects. Gain for the combined stimulus was somewhat higher for the lower frequencies and lower for the higher frequencies than gain for the disparity component alone; distinct differences were found between the phase of ocular vergence induced by the combined stimulus and by the disparity component alone. Phase lags were considerably smaller for the combined stimulus at all frequencies. These findings held for all subjects. They imply that ocular vergence tracking is more accurate in the natural situation where changing-size and

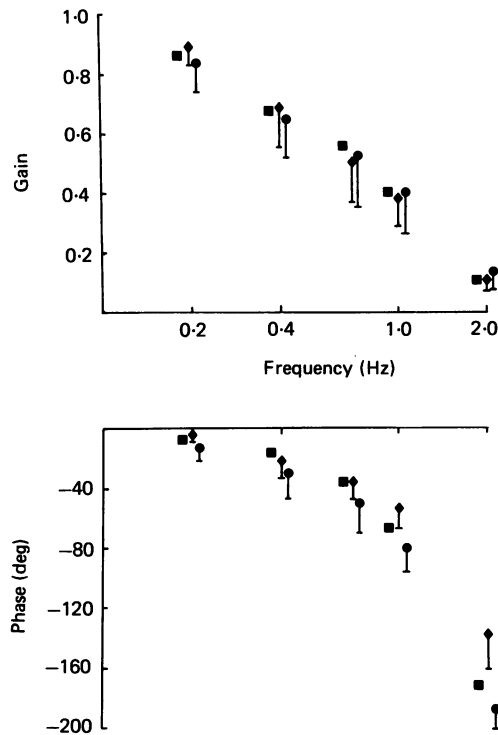


Fig. 7. Gain and phase of ocular vergence responses. Diamonds plot responses induced by a combination of disparity and size changes. Circles plot responses induced by the changing-disparity component alone. Squares plot theoretically predicted estimates for combined stimulation; these estimates were obtained by linearly adding the vergence responses induced by the disparity component alone and by the size component alone. Means and standard deviations are shown for five subjects.

changing-disparity stimulation are combined than in the laboratory situation when disparity alone is commonly used to explore dynamics of the vergence system.

It is widely supposed that the chief function of the vergence responses is to reduce retinal disparity, and indeed the case is well established for vergence changes induced by disparity alone. However, our finding that size change induces vergence movement raises some uncertainty about this supposition in the real-world visual situation where disparity changes are generally accompanied by size changes. With this in mind, we measured the vergence tracking errors while viewing oscillating disparity combined with oscillating size and during stimulation by the disparity component alone.

Table 3 shows that the binocular disparity was smaller for combined stimulation (i.e. vergence tracking was more accurate) than for stimulation with the disparity component alone. The difference between the binocular disparity in the two stimulus conditions was highly significant ( $P < 0.0005$ , Student's  $t$  test). This means that for fixation of a natural object moving in depth the presence of the changing-size component contributes significantly to the reduction of binocular disparity.

TABLE 3. Peak-to-peak amplitudes of binocular disparity during stimulation with disparity changes combined with size changes and during stimulation with the disparity component alone. Mean and standard deviations, in degrees, are shown for five subjects

Frequency (Hz)	Combined disparity and size	Disparity component alone
0.2	$0.43 \pm 0.20$	$0.68 \pm 0.28$
0.4	$1.11 \pm 0.43$	$1.36 \pm 0.56$
0.7	$1.67 \pm 0.35$	$1.92 \pm 0.51$
1.0	$2.15 \pm 0.23$	$2.50 \pm 0.18$
2.0	$2.68 \pm 0.15$	$2.75 \pm 0.23$

To investigate possible interactions between responses to changing disparity and responses to changing size, ocular vergence responses to the changing-size component (Fig. 3) and to the disparity component (Fig. 7) were added and compared with responses to combined stimulation. The differences between linearly predicted and measured response amplitudes were small compared to the size-induced vergence responses themselves, though the predicted gains were a little lower than experimental gains at the lower frequencies and a little higher at the higher frequencies. The linearly predicted phase lags were smaller than experimental phase lags for the lower frequencies and larger for the higher frequencies. The small inaccuracy in predicting gain was effectively cancelled by the small inaccuracy in predicting phase with the result that linearly predicted binocular disparity was about correct. The good agreement between predicted and measured responses implies that vergence responses to combined stimulation can be regarded as an approximately linear addition of responses to the separate disparity and size components of stimulation. If any interaction between changing size and changing disparity did occur, it was very weak.

#### *Smoothness of ocular vergence movements*

Several authors have noticed that stimulus-induced ocular vergence movements did not follow the stimulus smoothly but were somewhat irregular and oscillatory (Westheimer & Mitchell, 1956; Rashbass & Westheimer, 1961). This was observed during oscillatory as well as single step stimulation. We noted that in those experiments vergence movements were induced by pure changing disparity unaccompanied by any changing-size component.

We compared (a) the smoothness of ocular vergence movements induced by stimulation with a combination of disparity and changing size with (b) responses induced by stimulation with the disparity component alone. Ocular vergence was averaged over all the cycles of a measurement. The wave form and the standard deviations of the vergence oscillations gave direct information about the smoothness and reproducibility of the sinusoidal vergence movements. In addition to the averaged data, single (non-averaged) ocular vergence movements induced by ramp stimulation were compared for the two stimulus conditions.

Fig. 8 shows representative vergence movements recorded from one subject. For oscillatory stimulation, standard deviations were significantly smaller for combined disparity and size than for disparity stimulation alone (Fig. 8C). This held for all

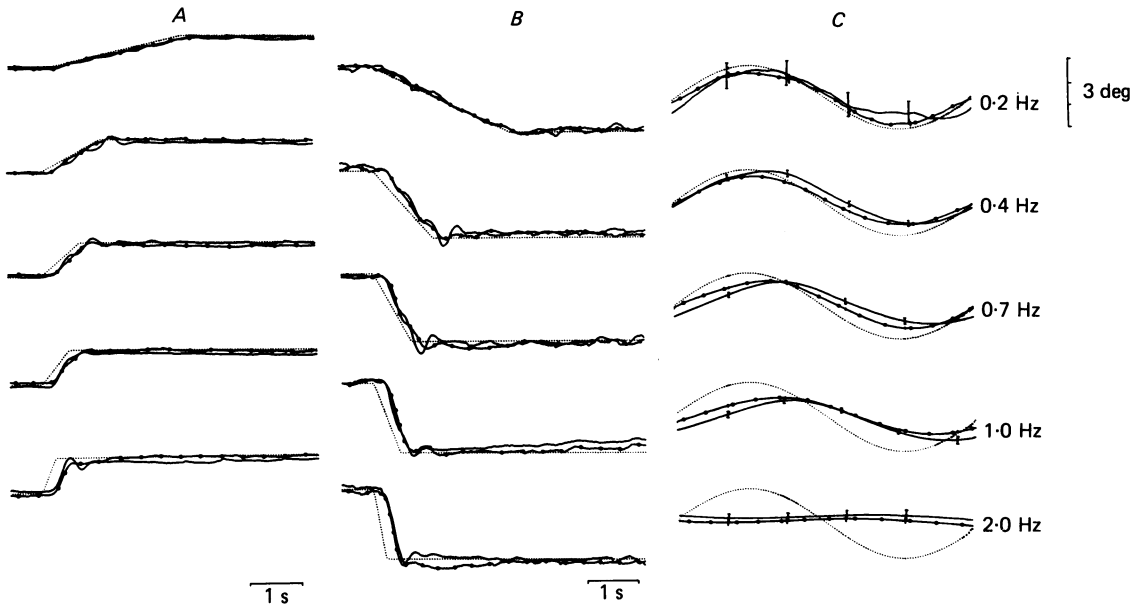


Fig. 8. Continuous lines with large dots plot ocular vergence movements induced by stimulation with changes of disparity combined with changes of size. Continuous lines without dots plot vergence movements induced by stimulation with the disparity component alone. *A*, the dotted lines indicate stimulus ramps equivalent to motion away from the observer. *B*, similar responses as in *A*, but the stimulus ramps (dotted lines) were equivalent to motion towards the observer. *C*, ocular vergence responses to oscillatory stimulation. Vertical bars indicate the standard deviations of responses induced by disparity alone. Signal-to-noise ratio was enhanced in *C* by averaging for 32.8 s (six to sixty response cycles, depending on the frequency). Note the different time scales for each frequency. Conventions as in Fig. 2.

subjects. Averaged trajectories of ocular vergence were less irregular and followed the stimulus with shorter phase lags for the combined stimulus than for the disparity component alone. Conclusions for single ramp movements were in agreement with the conclusions based on oscillatory stimulation (Fig. 8*A* and *B*). Noisy tracking errors observed during stimulation with pure disparity were mostly reduced or completely absent from movements during combined stimulation. (The amplitude difference between responses to receding and approaching ramps evident in Fig. 8*A* and *B* is of no immediate significance: in our experimental conditions, the rate of change of retinal image size was twice as great for approaching than for receding ramps.)

The accuracy of ocular vergence tracking for sinusoidal stimulation was quantified as follows: our rationale was that, if the eyes tracked an  $F$  Hz stimulus oscillation with high accuracy and little noise, then the total power present in the vergence responses would be concentrated in a narrow band of frequencies centred on  $F$  Hz, but if ocular tracking was inaccurate and noisy, then the power would spread over a wider band of frequencies. The ocular vergence movements were analysed by discrete Fourier transform and, after computation of the frequency band widths, the

TABLE 4. Percentages of the total power of ocular vergence movements contained within a band width of  $\pm 5\%$  around the frequency of stimulation during stimulation by oscillation of disparity combined with oscillations of size, and during stimulation by the disparity component alone. Means and standard deviations are shown for five subjects

Frequency (Hz)	Combined disparity and size (C)	Disparity component alone (D)	Difference between C and D
0.2	$92 \pm 6$	$87 \pm 8$	5
0.4	$90 \pm 10$	$80 \pm 10$	10
0.7	$83 \pm 12$	$68 \pm 17$	15
1.0	$67 \pm 19$	$48 \pm 18$	19
2.0	$21 \pm 12$	$14 \pm 9$	7

power contained within a frequency band width of  $\pm 5\%$  around the frequency of stimulation was calculated. Table 4 sets out percentages of this power relative to the total power of the ocular vergence movements in the two cases of combined stimulation and stimulation by the disparity component alone.

Table 4 shows that relatively more response power was contained within a narrow band around the stimulus frequency when disparity and size changed together than when the disparity component alone was the stimulus. Comparison of the power distributions in all five subjects with the Student's *t* test showed that this difference was highly significant ( $P < 0.001$ ). Since the power distribution was centred on the same frequency of stimulation for the two kinds of stimulation, the sharper concentration of power implied that the stimulus was followed more faithfully by the ocular vergence movements when the changing-size component was present than when it was absent. This improvement in the accuracy of ocular size tracking was not the same at all stimulus oscillation frequencies, however (Table 4, last column). The size component gave the greatest improvement in vergence tracking accuracy at a stimulus oscillation frequency of around 0.5 Hz, and at lower and higher frequencies the improvement was less. Noting that this frequency dependence resembles the frequency response of ocular vergence induced by changing-size stimulation alone (Fig. 4), we infer that the increased stability of ocular vergence was a direct result of the additional information contained in the independently processed changing-size component.

#### DISCUSSION

*The vergence system responds transiently to size alone and in a sustained manner to disparity alone*

We report here that vergence movements are induced by a rate of change of retinal image size in normal (i.e. closed-loop) viewing conditions.

The idea that the vergence response to size is a transient response with little, if any, sustained component can be supported by three lines of evidence. First, there is no appreciable sustained component in the vergence response to a ramp change of size; this observation is direct evidence that the response is effectively a pure transient (Fig. 6*A* and *C*). Secondly, the amplitude of the vergence responses to size oscillations has a bandpass characteristic, peaking at about 0.4 Hz (Fig. 3); if it is

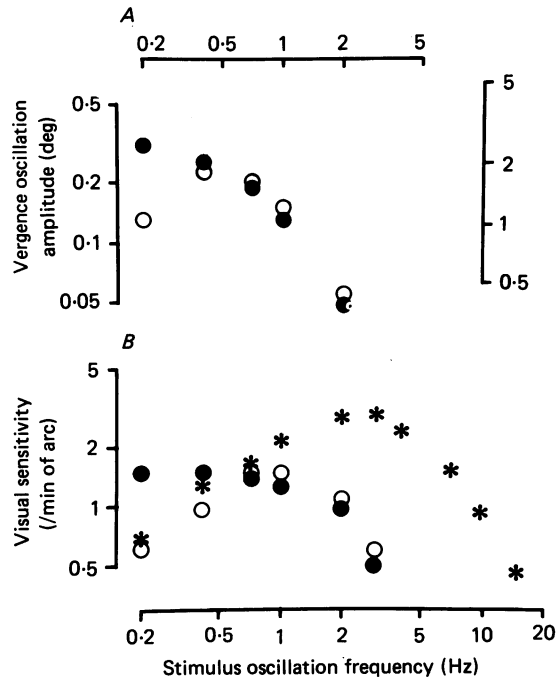


Fig. 9. *A*, left and right ordinates are amplitudes of vergence oscillations induced respectively by size oscillations and by disparity oscillations. Abscissa is stimulus oscillation frequency. Open circles plot responses to size oscillations, and filled circles plot responses to disparity oscillations. (Mean of five subjects, data of Fig. 3.) *B*, ordinate is psychophysical sensitivity (reciprocal of threshold). Abscissa is stimulus oscillation frequency. Open circles and filled circles are for motion-in-depth sensation induced by oscillating size and oscillating disparity respectively. Asterisks are for oscillating-size sensation induced by oscillating size. (Mean of three subjects, computed from data in Regan & Beverley, 1979.)

valid to extrapolate the low-frequency falloff below 0.2 Hz, then the Fig. 3 data imply that the sustained response to static size would be small or even absent. Thirdly, vergence oscillations induced by size oscillations have phase lags that can be explained by assuming the effective stimulus to be the instantaneous rate of change of size rather than the instantaneous size itself.

It is well established that the vergence response to changing disparity alone has a low-pass characteristic, with a sustained component, and a high-frequency rolloff (Zuber & Stark, 1968; Erkelens & Collewijn, 1985*b*). The data of Fig. 7 confirm these observations.

In order to compare vergence responses to size alone with vergence responses to disparity alone, we plotted the open-loop response amplitudes for the two stimuli on a single graph (Fig. 9*A*). This plot brings out the chief difference between the two kinds of vergence response: as stimulus oscillation frequency is reduced to low values, size responses attenuate (open symbols), but disparity responses do not attenuate (filled symbols).



Fig. 9*A* also indicates that, in our stimulus condition, disparity responses were considerably larger than size responses (compare left and right ordinates): vergence oscillations induced by oscillating size did not exceed 10% of the amplitudes of disparity-induced oscillations. However, before attaching undue significance to the comparative ineffectiveness of pure size changes, it should be noted that an isolated isotropic size change is no more common in the natural world than is an isolated change of disparity. Furthermore, for geometrical reasons, disparity change is favoured over size change when the target is of small linear dimensions; for a sufficiently large object the balance is reversed, and changing size is favoured over changing disparity, but note that this is a consequence of geometry rather than of physiology (Regan & Beverley, 1979). This is because the relative amplitudes of the size and disparity components of retinal image change are not fixed, but depend on the object's linear dimensions and the observer's interpupillary separation (but not on the viewing distance, although this assumes that the viewing distance is considerably greater than both the interpupillary distance and the object's width, and is generally true only for rigid, non-rotating objects) (Regan & Beverley, 1979). In any case, the 10:1 ratio of comparative effectiveness is not out of line with comparable psychophysical data; when we normalize the psychophysical data on the basis of our present stimulus geometry, we find that psychophysical sensitivity to size oscillation was from two to eleven times less than psychophysical sensitivity to disparity oscillation for the three subjects of Fig. 9*B* (data derived from Regan & Beverley, 1979).

#### *The inherent ambiguity of the size changes*

Poincaré (1913) pointed out that an increase of an object's retinal image size is ambiguous: it might mean that the object is approaching; it might mean that the object is non-rigid and is growing in size; or it might signify a combination of motion in depth and non-rigidity. There is psychophysical evidence that the human visual system resolves the problem by responding to the ambiguous stimulus as though it were produced by object motion-in-depth response rather than by a change in object size. (This stereotype response only occurs providing that rigidity and non-rotation conditions are obeyed (Beverley & Regan, 1980).) It must be admitted that a visual system biased to signal the approach of a predator when the retinal image expanded isotropically would produce incorrect signals from time to time. On the other hand, the errors would not usually be serious, and the bias might confer an evolutionary advantage over an alternative visual system that submitted for cognitive decision the alternative possibilities that the predator was rapidly expanding or rapidly approaching.

It is more difficult to establish whether or not the vergence system can resolve Poincaré's ambiguity. However, an indication that vergence responses also correspond to motion-in-depth rather than to changing-size signals is provided by our present finding that vergence responses to size oscillations peak at about 0.5 Hz and grow progressively weaker as oscillation frequency rises, falling by more than threefold between 0.5 and 1.0 Hz (Fig. 9*A*, open circles). This bandpass characteristic closely resembles the effect of frequency on the sensation of motion in depth produced by size oscillations (Fig. 9*B*, open circles), but is quite different from the effect of

frequency on the sensation of changing size produced by the same stimulus (Fig. 9B, asterisks).

### *Shape changes and size changes*

Researchers in computational vision have paid considerable attention to the problem of object rigidity; the problems faced by the visual system in segregating an object from its background, and in establishing the object's motion are much simplified when the object in question can be assumed to be rigid and non-rotating (Ullman, 1979; Longuet-Higgins & Prazdny, 1980; Marr, 1982). In responding to an object's motion in depth, the ocular vergence system is faced with problems of segregating figure from ground and of estimating its speed and direction of motion that are similar to problems that have been extensively discussed in the context of computational vision and perception. Our evidence on vergence responses to one-dimensional size changes bears on this issue of object rigidity and figure-ground segregation.

When a rigid, non-rotating rectangular object of side lengths  $L_1$  and  $L_2$  moves towards the eye, the rate of change of size in its retinal image depends uniquely on azimuth. In particular, the ratio (linear rate of change of size parallel to side  $L_1$ )/(linear rate of change of size parallel to  $L_2$ ) is equal to the ratio  $L_1/L_2$ : this retinal image property is characteristic of a rigid, non-rotating, effectively flat object (Beverley & Regan, 1980). It has been found that visual responses to a square whose magnification changes isotropically differ considerably from visual responses to a square whose size changes along only one dimension (Beverley & Regan, 1980). Furthermore, there is a non-linear interaction between size changes along perpendicular directions; and, for a rectangular target, this interaction is maximal if the condition for a non-rotating, rigid object is fulfilled, i.e. if the orthogonal rates of change of size are in the inverse ratio of the side lengths (Beverley & Regan, 1980). This finding is consistent with the idea that the visual system makes a distinction between, on the one hand, moving objects that are rigid and non-rotating and, on the other hand, moving objects that are non-rigid or rotating.

Our vergence data reported above lead to a similar conclusion for the ocular vergence system. So far as the optical stimulus is concerned, the sum of separate height and width oscillations is exactly equivalent to the isotropic oscillation of size. No such linear equivalence was evident in eye movements induced by changing size: at a frequency of 0.4 Hz, for example, oscillating height alone gave only 1.0 min of arc and oscillating width alone gave only 0.9 min of arc, but isotropic oscillations of size produced vergence oscillations of amplitude 13.9 min of arc (Table 2). The large vergence response to the combined height and width oscillations implies a strong non-linear facilitation whose effect is that the vergence response to isotropic size change is up to seven times stronger than would be expected assuming simple linear summation. We conclude that the vergence system responds weakly to the isolated height or isolated width oscillations that are characteristic of a rotating or non-rigid object. Following a previous argument (Beverley & Regan, 1980), this non-linear facilitation might reflect a functional property of the vergence system whose effect is to create a differential response to rigid, non-rotating objects and to non-rigid or rotating objects. Such a non-linearity might be regarded as, in effect, 'recognizing'

rigid, non-rotating objects by its selective 'blindness' to non-rotating or non-rigid objects.

### *Control experiments*

Now we turn to the question of whether vergence responses to dynamically changing size are genuine responses to size rather than being responses to covarying parameters. In our present study, luminance was held constant so that we can reject luminance-induced responses as a possible contaminant. Nevertheless, we must consider changes of total light flux as a possible contaminant; because luminance was held constant, total light flux necessarily increased as the square expanded, and decreased as the square contracted. We can, however, reject the possibility that flux changes were responsible for the stimulus-induced vergence oscillations, because a control experiment showed that, by itself, flicker did not drive vergence (Fig. 5*D*).

A problem that has already been mentioned is that vergence motion induced by size changes in ordinary viewing conditions might be contaminated by responses to changing disparity because the vergence movements induced by the size changes cause the squares' retinal images to translate, even though the squares themselves are stationary. In order to remove this contamination we arranged that the displayed squares translated at a speed that exactly matched the eyes' vergence movements, so that the retinal images did not move horizontally even though the eyes were moving. We found that size changes unaccompanied by disparity changes induced clear vergence movement in these open-loop viewing conditions (Fig. 3).

The results of this experiment have further implications, however. Although the square's disparity was undoubtedly oscillating in the normal (i.e. closed-loop) viewing condition, vergence oscillations were the same in open-loop and closed-loop conditions for disparity, implying that the disparity oscillations produced no vergence response at all. This is surprising because we know not only that disparity oscillations could drive vergence oscillations in our experimental conditions (Fig. 7), but in fact drove them about ten times more strongly than did size oscillations alone (Fig. 9*A*, compare ordinates). It seems, then, that although vergence movement can be induced by disparity changes caused when some outside agency moves a target across the retina, disparity changes that arise from internally generated eye movements do not drive vergence changes at all. It remains to be shown whether this conclusion holds only for vergence movements induced by changing size or whether it might also hold for vergence movements induced by changes in accommodation.

The relationship between size-induced vergence and accommodative vergence is not clear. Unfortunately, our present evidence does not offer a clear differentiation between the following two alternatives: (a) an isotropic rate of change of retinal image size drives vergence directly, or (b) indirectly via the accommodation mechanisms. If one wished to argue for an indirect effect, the data of Figs. 3 and 6 require that the relevant hypothetical effect of size on accommodation be entirely transient with no sustained component. Furthermore, it would be necessary to place a strong non-linearity peripheral to the accommodation mechanism because, as noted above, isotropically changing size drives vergence much more strongly than the sum of physically equivalent one-dimensional changes of size.

One possible means of differentiating between these two possibilities might be to

compare the dynamic properties of vergence responses to changing size, with the dynamics of the accommodative responses to changing size. Unfortunately, the accommodative data do not seem to have been published. The nearest available equivalent is measurements of accommodative oscillations induced by an acuity target that was oscillated mechanically in depth (Campbell, Robson & Westheimer, 1959). Accommodation, measured by means of an infra-red optometer (Campbell & Robson, 1959) seems to have followed stimulus oscillations up to frequencies somewhat beyond those to which we were able to drive vergence by stimulating with oscillating size (Fig. 4). In addition, Campbell *et al.* (1959) give the time delay of the accommodative oscillations as 400 ms, which is considerably longer than our 204 ms delay for vergence oscillations (see Results). But, in view of possible intersubject differences and differences in data analysis between the two studies, no firm conclusions are possible. However, it does seem technically possible to resolve this question by experimentally correlating the vergence responses induced by changing size with simultaneously recorded accommodative responses.

*Vergence responses to simultaneous changes of disparity and size*

In this section we discuss the finding that vergence tracking is more accurate and less noisy when disparity and size change together than when disparity alone changes. This finding suggests that the role of changing size in the control of ocular vergence may only be evident when size change is combined with disparity change.

The improvement in vergence tracking accuracy that we observed when size change accompanied disparity change (see Results) can be at least partially understood in terms of the effect of the added changing-size component on the phase of the vergence response. The time delay between the velocity of the change in size and the ocular vergence response was about the same as the latency between target and ocular vergence for changing disparity (Erkelens & Collewijn, 1985*b*). This implies that changing size introduced a velocity-sensitive component to ocular vergence which speeded up the movements.

The similar time delays for responses to changing size and to changing disparity might create the false impression that neural processes underlying the two responses have the same processing times. If the rate of the changing target size is the effective input for the changing-size system as was suggested by the phase relation between the changing-size stimuli and the ocular vergence responses, then the latencies can easily be computed from these phase relations (Fig. 3). The calculated values of the time delays for different frequencies of stimulation are shown in Table 5. The calculated time delays do not depend on the stimulus frequency and have durations between 194 and 230 ms (except at 0.2 Hz where the phase may be unreliable). Since the changing-disparity system is a closed-loop system, time delays between stimulus and response cannot be directly computed from the phase relations presented in Fig. 7. Suppose that the target vergence ( $V_t$ ) changes as follows

$$V_t(t) = A \sin(\omega t),$$

where  $A$  is the amplitude,  $\omega$  the frequency in rad/s and  $t$  is time. If it is assumed that the ocular vergence ( $V_o$ ) follows the target vergence according to a sinusoidal wave form with amplitude  $B$  and phase shift  $\phi$ , then  $V_o$  can be expressed as

$$V_o(t) = B \sin(\omega t + \phi).$$

TABLE 5. Amplitude and phase of the retinal stimulus and ocular vergence response. The amplitudes of retinal disparity are expressed in percentages relative to the target vergence amplitudes. Phase is expressed in degrees relative to the phase of target vergence. The amplitude and phase of vergence responses were computed from the data presented in Figs. 3 and 7. Latency was estimated from the slope of the phase *versus* frequency characteristic

Stimulus	Frequency (Hz)	Phase of rate of size change	Phase of ocular vergence	Latency (ms)
Size	0.2	90	65	347
oscillations	0.4	90	59	215
	0.7	90	32	230
	1.0	90	20	194
	2.0	90	-65	215

Stimulus	Frequency (Hz)	Amplitude of disparity	Phase of disparity	Phase of ocular vergence	Latency (ms)
Disparity	0.2	28	46	-14	833
oscillations	0.4	54	34	-29	438
	0.7	79	32	-52	333
	1.0	102	21	-82	286
	2.0	112	-1	-192	265

This results in a retinal disparity change ( $D$ ) given by

$$D(t) = V_t(t) - V_o(t) = A \sin(\omega t) - B \sin(\omega t + \phi).$$

This equation can be rewritten as

$$D(t) = A [\sin(\omega t) - G \sin(\omega t + \theta)] = AC \sin(\omega t + \theta),$$

where  $G$  is the gain of ocular vergence in relation to target vergence, and  $C$  and  $\theta$  are respectively the amplitude and phase of the disparity relative to the target vergence. Since  $G$  and  $\phi$  are known,  $C \sin(\omega t + \theta)$  can be computed by vectorial subtraction of  $G \sin(\omega t + \phi)$  from  $\sin(\omega t)$  in the vector field of which  $\sin(\omega t)$  and  $\cos(\omega t)$  are the orthogonal unit vectors. Table 5 shows the computed values of  $C$  and  $\theta$  based upon the values of  $G$  and  $\phi$  obtained from the gain-phase relations of ocular vergence in case of changing-disparity stimulation alone (Fig. 7). It shows that the disparity leads the target vergence for all frequencies of stimulation, except for the frequency of 2.0 Hz. The latencies of ocular vergence in response to retinal disparity (the actual stimulus) are far longer than those for changing size, especially for the lower frequencies, and strongly depend on the amplitude of the disparity. In the present experiments the phase shifts between the changing-disparity stimuli and the ocular vergence movements were larger and more dependent on the frequency than in those of Rashbass & Westheimer (1961) who stimulated with sinusoidally changing disparities superimposed on stabilized retinal images. The difference might be explained by the fact that the changing-disparity stimuli used by Rashbass & Westheimer (1961) had the same amplitude for all frequencies, while the amplitudes calculated in Table 5 changed considerably as a function of frequency. The computed latencies of the fusional vergence system do not indicate the existence of a predictive operator in the system which would achieve shorter latencies in case of predictable stimuli, as proposed by Krishnan, Farazian & Stark (1973).

One of the important factors that affect the dynamic stability of a feed-back system is its latency or dead time. Thus, there may be a relation between the long latencies in the fusional vergence system and the oscillations in the ocular vergence movements during stimulation with changing disparity alone (Fig. 8). If this relation really exists, then the reduction of the oscillations as a result of concomitant changing-size stimulation is explained by the stabilizing influence of changing size due to the shorter latencies of this system. Westheimer & Mitchell (1956) have suggested that the oscillations in the ocular vergence movements were caused by the absence of a stimulus for accommodation. In their experiments, however, changing-size stimulation was also missing. The almost complete absence of oscillations in ocular vergence movements induced by the combination of changing-size and changing-disparity stimulation without stimulation of accommodation suggests that changing size is more likely to contribute to the stabilization of ocular vergence than stimulation of accommodation.

*The dynamic characteristics of vergence and sensation compared*

A series of psychophysical papers present evidence that changing size is processed independently of translational motion (Regan & Beverley, 1978, 1980), that changing disparity is processed independently of static disparity (Beverley & Regan, 1973; Richards & Regan, 1973), and that changing size is processed independently of changing disparity (Regan & Beverley, 1979). At a physiological level, there is evidence that the human vergence system processes static and changing disparity rather independently (Regan, Erkelens & Collewijn, 1986*b*), single-unit electrophysiology in animals has provided evidence for cortical neurones sensitive to changing disparity and to the direction of motion in depth (Pettigrew, 1973; Zeki, 1974; Cynader & Regan, 1978; Poggio & Talbot, 1981), and neurones in cortex (Zeki, 1974; Regan & Cynader, 1979) and in the Clare-Bishop area (Toyama & Kozasa, 1982) with the required non-linearity to confer specific sensitivity to changing size.

With the aim of more closely comparing vergence data with previous psychophysical data we used the same stimulus display generator as that used in the psychophysical studies, though only one subject (D.R.) served in both studies. Although they are very different measures of visual performance, the dynamic properties of vergence and sensation showed several rather close correlations; as noted below, there was only one significant disagreement.

Fig. 9*A* and *B* allows the effects of size oscillation frequency to be compared for vergence oscillation amplitude and visual psychophysical sensitivity (open circles); a similar comparison between vergence and sensory mechanisms can also be made for disparity oscillations (filled circles). The shapes of the eye movement and psychophysical curves are remarkably similar, especially in view of the fact that the ordinates in Fig. 9*A* are amplitudes while the Fig. 9*B* ordinate is sensitivity, and that the vergence data points are means for five subjects recorded in Rotterdam, while the psychophysical data points are means for three different subjects recorded seven years earlier in Canada.

For motion-in-depth sensation, as for eye movements, responses to oscillating size have a bandpass characteristic that is consistent with a transient system possessing little or no sustained component (Fig. 9*A* and *B*, open circles). The curves differ in

one minor respect only; the psychophysical plot is bodily displaced to slightly higher frequencies. This difference, however, is no larger than intersubject variability. Additional evidence that the vergence responses to size are transient, being determined by the rate of change of size is discussed in Results above; additional evidence that motion-in-depth perception is also rate dependent is discussed elsewhere (Beverley & Regan, 1979). A further correlation between sensation and vergence responses to size changes is the superiority of binocular over monocular stimulation: binocular thresholds for motion in depth are lower than monocular thresholds (Regan & Beverley, 1979, Table 1), and larger vergence responses are produced by binocular stimulation (see Results).

The dynamic characteristic of eye movements and of perception are also similar when changing disparity is the inducing stimulus. Disparity sensitivity has a low-pass characteristic for motion-in-depth perception consistent with a sustained system, just as is the case for vergence responses to disparity (Fig. 9A and B, filled circles) (Regan & Beverley, 1978, 1979, 1980; Beverley & Regan, 1979, 1980; Regan, 1986).

Next we discuss evidence that, at an early stage, changing disparity and changing size are processed substantially independently. For real-world objects, size and disparity information generally agree in the sense that both signify 'towards' or both signify 'away'. In the laboratory, however, it is possible to pit one against the other. In this situation, it is possible to cancel the sensation of motion-in-depth (though, for the subjects of Fig. 9B, cancellation required from two to nine times greater change of size relative to the change of disparity than would be the case for a corresponding real-world object). This finding was taken as one of several items of evidence for a hypothesis, according to which size change and disparity change are processed independently in parallel, giving rise to two signals that subsequently converge at a stage whose output determines the sensation of motion in depth (Regan & Beverley, 1979). Above we report evidence that vergence responses to changes of size and disparity are approximately independent, thus paralleling the psychophysical findings: vergence oscillation amplitude induced by combined stimulation is closely equal to the sum of the amplitudes of the two stimulus components alone (see Results).

There is, however, one exception to the close correlation between the characteristics of vergence motion and of motion-in-depth perception. Changing the disparity of a stereoscopically viewed dot pattern does not induce a sensation of motion-in-depth unless a reference mark is present in the visual field. On the other hand, the same stimulus induces strong vergence movements when no reference mark is visible even though there is no sensation of motion in depth (Erkelens & Collewijn, 1985*a, b*; Regan, Collewijn & Erkelens, 1985). These authors showed that, although disparity-induced vergence movements are driven by absolute retinal disparity, the sensation of motion in depth requires a change in relative disparities between different targets in the visual field. This lack of correlation is not observed for changing-size stimulation since, by definition, changing size comprises relative motion; neither vergence responses nor motion-in-depth sensation is affected by removing reference marks from the visual field (Regan, Erkelens & Collewijn, 1986*a, b*).

In order to account for the psychophysical data on size changes, it has been hypothesized that the first stage of processing size-change information is functionally

equivalent to taking the local values of  $\text{div } \mathbf{V}$  in the velocity field of the retinal image (Longuet-Higgins & Prazdny, 1980). (In principle there is some advantage in describing the retinal flow field in the notation of vector analysis rather than in terms of local values of velocity  $\mathbf{V}$ ; for example, the vector quantities  $\text{div } \mathbf{V}$  and  $\text{curl } \mathbf{V}$  are invariant with eye rotation, while  $\mathbf{V}$  is not invariant. It should be noted, though, that to hypothesize a functional equivalent is not to imply that neural mechanisms physically compute, for example, line integrals.) It has been further suggested that this functional equivalence might be physically achieved by an ensemble of elements, each of which is sensitive to the difference between the velocities at two different retinal locations (Regan & Beverley, 1979, 1980; Beverley & Regan, 1980; Regan, 1985); according to this suggestion, there is a non-linear interaction between the outputs of elements sensitive to different directions of motion that favours isotropic retinal image expansion and rejects any retinal image shape changes that are characteristic of a rotating or non-rigid object. The close parallels between vergence and psychophysical data reported above and, in particular, our evidence that vergence responses show a strong non-linearity of the required kind, suggest that a first attempt to model vergence responses to size changes might use as a basis the model proposed to explain psychophysical responses to size changes.

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#### REFERENCES

- ALPERN, M. (1958). Vergence and accommodation: can change in size induce vergence movements? *Archives of Ophthalmology* **60**, 355-357.
- BEVERLEY, K. I. & REGAN, D. (1973). Evidence for the existence of neural mechanisms selectively sensitive to the direction of movement in space. *Journal of Physiology* **235**, 17-29.
- BEVERLEY, K. I. & REGAN, D. (1979). Separable aftereffects of changing-size and motion in depth: different neural mechanisms? *Vision Research* **19**, 727-732.
- BEVERLEY, K. I. & REGAN, D. (1980). Visual sensitivity to the shape and size of a moving object: implications for models of object perception. *Perception* **9**, 151-160.
- CAMPBELL, F. W. & ROBSON, J. G. (1959). High-speed infrared optometer. *Journal of the Optical Society of America* **49**, 268-272.
- CAMPBELL, F. W., ROBSON, J. G. & WESTHEIMER, G. (1959). Fluctuations of accommodation under steady viewing conditions. *Journal of Physiology* **145**, 579-594.
- COLLEWIJN, H., VAN DER MARK, F. & JANSEN, T. C. (1975). Precise recording of human eye movements. *Vision Research* **15**, 447-450.
- COLLEWIJN, H., VAN DER STEEN, J. & STEINMAN, R. M. (1985). Human eye movements associated with blinks and prolonged eye-lid closure. *Journal of Neurophysiology* **54**, 11-27.
- CYNADER, M. & REGAN, D. (1978). Neurones in cat parastriate cortex sensitive to the direction of motion in three-dimensional space. *Journal of Physiology* **274**, 549-569.
- ERKELENS, C. J. & COLLEWIJN, H. (1985a). Motion perception during dichoptic viewing of moving random-dot stereograms. *Vision Research* **25**, 583-588.
- ERKELENS, C. J. & COLLEWIJN, H. (1985b). Eye movements and stereopsis during dichoptic viewing of moving random-dot stereograms. *Vision Research* **25**, 1689-1700.
- FINCHAM, E. F. (1951). The accommodation reflex and its stimulus. *British Journal of Ophthalmology* **35**, 381-393.



- FINCHAM, E. F. & WALTON, J. (1957). The reciprocal actions of accommodation and convergence. *Journal of Physiology* **137**, 488–508.
- ITTLESON, W. H. & AMES, A. (1950). Accommodation, convergence and their relation to apparent distance. *Journal of Psychology* **30**, 43–62.
- KENYON, R. V., CIUFFREDA, K. J. & STARK, L. (1978). Binocular eye movements during accommodative vergence. *Vision Research* **18**, 545–555.
- KRISHNAN, V. V., FARAZIAN, F. & STARK, L. (1973). An analysis of latencies and prediction in the fusional vergence system. *American Journal of Optometry and Archives of the American Academy of Optometry* **50**, 933–939.
- LONGUET-HIGGINS, H. C. & PRAZDNY, K. (1980). The interpretation of a moving retinal image. *Proceedings of the Royal Society B* **208**, 385–397.
- MARR, D. (1982). *Vision*. San Francisco: Freeman.
- PETTIGREW, J. D. (1973). Binocular neurons which signal changes of disparity in area 18 of cat visual cortex. *Nature* **241**, 123–124.
- POGGIO, G. F. & TALBOT, W. H. (1981). Mechanisms of static and dynamic stereopsis in foveal cortex of the rhesus monkey. *Journal of Physiology* **315**, 469–492.
- POINCARÉ, H. (1913). *The Value of Science*. New York: Science Press.
- RASHBASS, C. & WESTHEIMER, G. (1961). Disjunctive eye movements. *Journal of Physiology* **159**, 339–360.
- REGAN, D. (1986). Visual responses to four kinds of relative motion. *Vision Research* **26**, 127–145.
- REGAN, D. & BEVERLEY, K. I. (1978). Looming detectors in the human visual pathway. *Vision Research* **19**, 415–421.
- REGAN, D. & BEVERLEY, K. I. (1979). Binocular and monocular stimuli for motion in depth: changing-disparity and changing-size feed the same motion-in-depth stage. *Vision Research* **19**, 1331–1342.
- REGAN, D. & BEVERLEY, K. I. (1980). Visual responses to changing size and to sideways motion for different directions of motion in depth. *Journal of the Optical Society of America* **70**, 1289–1296.
- REGAN, D., COLLEWIJN, H. & ERKELENS, C. J. (1985). Necessary conditions for motion in depth perception. *Investigative Ophthalmology and Visual Science (ARVO supplement)* **26**, 242.
- REGAN, D. & CYNADER, M. (1979). Neurons in area 18 of cat visual cortex selectively sensitive to changing size: nonlinear interactions between the responses to two edges. *Vision Research* **19**, 699–711.
- REGAN, D., ERKELENS, C. J. & COLLEWIJN, H. (1986*a*). Necessary conditions for motion in depth perception. *Investigative Ophthalmology and Visual Science* **27**, 584–597.
- REGAN, D., ERKELENS, C. J. & COLLEWIJN, H. (1986*b*). Visual field defects for vergence eye movements and for stereomotion perception. *Investigative Ophthalmology and Visual Science* (in the Press).
- RICHARDS, W. & REGAN, D. (1973). A stereo field map with implications for disparity processing. *Investigative Ophthalmology* **12**, 904–909.
- ROBINSON, D. A. (1963). A method of measuring eye movement using a scleral coil in a magnetic field. *IEEE Transactions on Biomedical Electronics* **BME-10**, 137–145.
- SEMMLOW, J. L. & WETZEL, P. (1979). Dynamic contributions of the components of ocular vergence. *Journal of the Optical Society of America* **69**, 639–645.
- TOYAMA, K. & KOZASA, T. (1982). Responses of Clare-Bishop neurons to three dimensional movement of a light stimulus. *Vision Research* **22**, 571–574.
- ULLMAN, S. (1979). *The Interpretation of Visual Motion*. Boston: MIT Press.
- WESTHEIMER, G. & MITCHELL, D. E. (1956). Eye movement responses to convergent stimuli. *Archives of Ophthalmology* **55**, 848–856.
- WHEATSTONE, C. (1852). Contributions to the physiology of vision. II. *Philosophical Transactions of the Royal Society B* **142**, 1–18.
- ZEKI, S. M. (1974). Cells responding to changing image size and disparity in the cortex of the rhesus monkey. *Journal of Physiology* **242**, 827–841.
- ZUBER, B. L. & STARK, L. (1968). Dynamic characteristics of the fusional vergence eye-movement system. *IEEE Transactions on Systems and Scientific Cybernetics* **SSC-4**, 72–79.